THE STEM ANATOMY OF RESTIO TRITICEUS ROTTB., BOBARTIA INDICA L., AND CADABA JUNCEA (SPARM.) HARV.

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The flora of South Africa contains a wealth of material worthy of the attention of the anatomist, yet the structure of very few species has been described in detail. The three species described in the present paper have little in common save that they all show xeromorphic features.

RESTIO TRITICEUS Rottb.

The anatomy of the Restionaceae has been treated on a comparative basis by Solereder and Meyer (1929), who also reviewed the results of earlier investigations in this family. There is, however, no readily accessible account in English of the detailed structure of any single named species.

Restio triticeus, a common member of the Western Cape heath community, exemplifies many of the anatomical peculiarities of the Restionaceae. This plant is low-growing, stiff and erect, with a tough, wiry stem. The internodes are long and the nodes are enclosed by brown scarious bracts.

The internal structure of the stem comprises three well defined zones: a thick epidermis, a palisade and an inner core of mechanical and conducting tissue. The general structure is shown diagrammatically in Fig. 1 and a more detailed drawing of the outer tissues is shown in Fig. 2.

The epidermis is made up of large cells, somewhat elongated radially. The outer walls are extremely thick and this thickening extends to a lesser degree down the radial walls. The thickening is accompanied by cutinisation but no lignification takes place. The outer surface of the epidermis is covered by a moderately thick cuticle. On the lower parts of the stem, near ground level, many of the epidermal cells form blunt protruberances, making the surface distinctly scabrid (Figs. 3 and 4). The cuticle and epidermis, even in the young plant, give a strong reaction for tannin.

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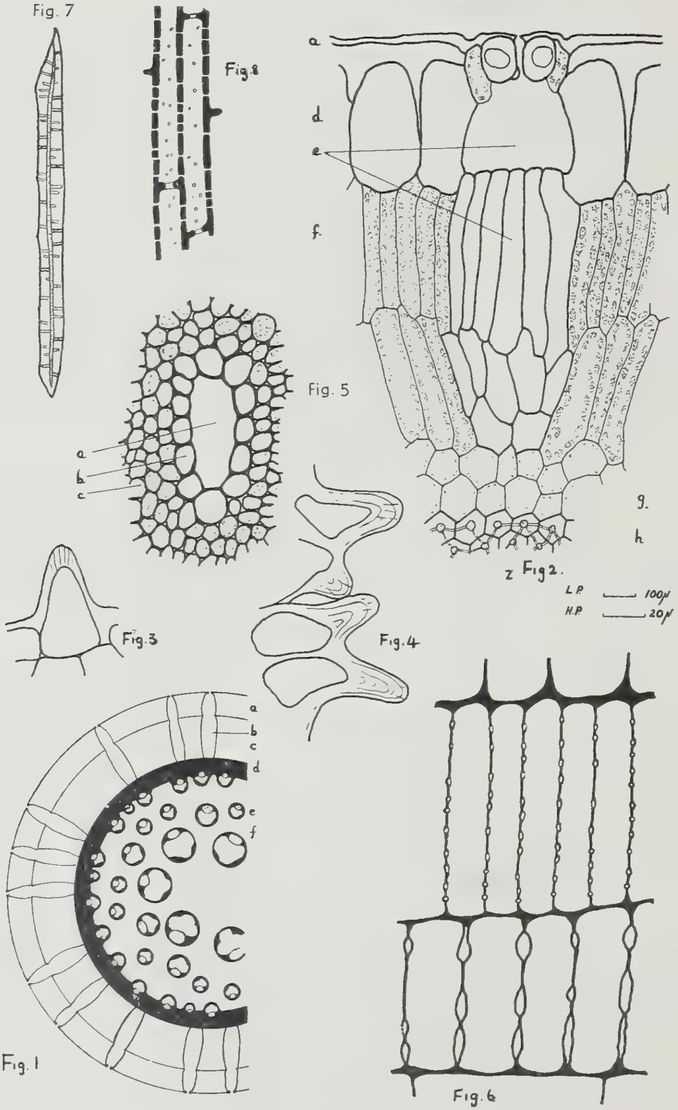


Figs. 1—8.—The stem anatomy of *Restio triticeus*. 1. Diagram of the distribution of the tissues as seen in transverse section: a, epidermis; b, sub-stomatal cavity; c, palisade; d, sclerenchyma; e, vascular bundle; f, ground tissue. Fig. 2. Detailed drawing of part of the outer tissues of the stem: a, cuticle; b, guard cell; c, accessory cell; d, epidermis; e, sub-stomatal cavity; f, palisade; g, parenchyma; h, sclerenchyma. Figs. 3 and 4. Epidermal hairs from the lower part of the stem. Fig. 5. Tangential section through a sub-stomatal cavity at the level of the palisade: a, cavity; b, mechanical cells; c, palisade cells. Fig. 6. Wall structure of the palisade, as seen in transverse section. Fig. 7. Fibre from sclerenchyma sheath. Fig. 8. Thick-walled parenchyma of ground tissue, as seen in longitudinal section.

The surface of the stem is raised into minute mounds, on to each of which a stoma opens. The mouths of the stomata are orientated to lie across the long axis of the stem. Each is accompanied by two accessory cells which are parallel to and slightly shorter than the guard cells, that is the stomata are of the paracytic type. The guard cells have thick cutinised walls whereas the accessory cells are thin-walled and non-cutinised.

A characteristic feature of the genus *Restio* is the possession of long, cylindrical sub-stomatal cavities, extending radially inwards and traversing the palisade layer. These cavities are in two sections, the outer bounded by epidermal cells and the longer, inner section supported by special mechanical cells (Fig. 5). There is a slight constriction between these two regions. The mechanical cells occur in two or three series, those immediately beneath the epidermis being considerably elongated, whilst those seated deeper are shorter and somewhat irregular in shape. They are all empty cells with relatively thin walls, impregnated with cutin.

The palisade consists of two rows of radially elongated cells containing abundant discoid chloroplasts. The cells have thin cellulose walls with simple pits. They are densely filled with cytoplasm and have large nuclei. A strong tannin reaction is given by these cells, especially in the young stem. The outer rows of palisade cells are separated from each other by slight convolutions of the walls, which gives the walls between adjacent cells a beaded appearance. The inner cells have much larger and more irregular protuberances on the walls and are therefore more widely separated from each other (Fig. 6).

Within the palisade is a zone of parenchyma, one to three cells deep. These are living cells with nuclei and cytoplasm. They are somewhat elongated in the direction of the axis. The walls are fairly thick but unlignified. In young stems this zone is very conspicuous, consisting of a single row of large colourless cells which separate the palisade from the inner woody core.

A sheath of five to eight rows of sclerenchyma fibres form the main supporting tissue of the stem. These are closely packed cells, hexagonal in transverse section of varying length and with either blunt or pointed ends. The thick, lignified walls show conspicuous lamellations and are perforated by numerous pit canals (Fig. 7). These canals connect the narrow lumen of adjacent cells. In many cases these cells appear to have nuclei and cytoplasmic contents, the latter being continuous from cell to cell. In young stems this region is also a site of tannin accumulation.

The central part of the stem is occupied by numerous vascular bundles embedded in a more or less lignified ground tissue. The vascular bundles are of the usual monocotyledonous type. There is a thin sheath of fibres, a strand of phloem, two large metaxylem vessels with tracheids between and a group of protoxylem vessels. The protoxylem vessels have annular thickening and occasionally give rise to lysigenous canals. A single series of small vascular bundles is embedded in the inner edge of the sclerenchyma zone whilst in the centre of the stem are twenty to forty scattered bundles of various sizes.

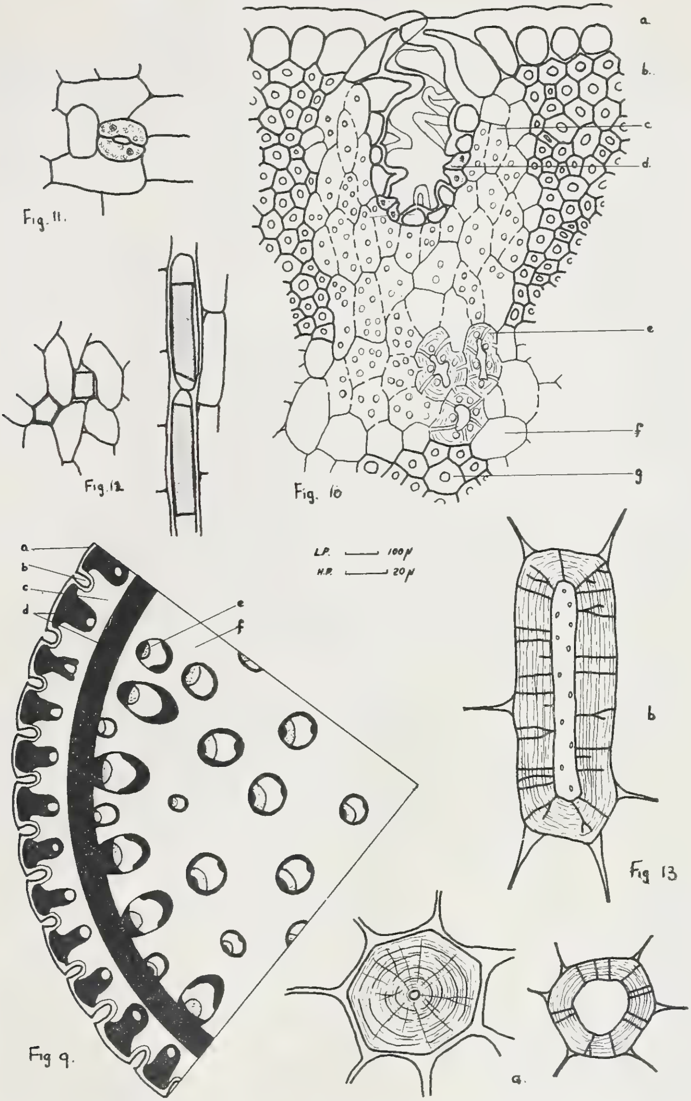
The ground tissue in which the vascular bundles are embedded consists of large, fairly thick-walled parenchyma cells (Fig. 8). These are living cells, highly vacuolated and containing starch. They are elongated in the direction of the axis and have transverse end walls. The innermost cells are the largest, being wider and shorter than the surrounding ones. Their walls are thin and have a tendency to break down and give rise to cavities in the centre of the stem. The peripheral cells, that is adjoining the sclerenchyma, may show some lignification, especially in the middle lamellae. The lignification is greatest in the lower parts of the stem, where the sclerenchyma and central vascular core form a single tough strand permeated by sclerotic cells.

BOBARTIA INDICA L.

Robartia indica has a short, swollen, branched woody rhizome from which arise tufts of stiff, rush-like leaves and flowering stems. The leaves are closely wrapped around the bases of the stems and in the upper parts are externally very similar to the stems. Inflorescences are borne near the apices of the stems and are surmounted by short, stiff spathes. It is the anatomy of the aerial stem which is described here. (See Figs. 9 and 10.)

The epidermis consists of large cells, the outer and radial walls of which are highly cutinised. Tannin may be detected in these cells but there is no lignification. The extremely thick cuticle gives a very strong fat reaction.

The surface of the stem shows fine longitudinal striations caused by the presence of stomatal furrows. These are lined by a continuation of the epidermis, the cells of which are thick-walled but smaller than those on the outer surface of the stem. They differ also in that many of them are prolonged into blunt hairs which project into the cavities of the furrows. Owing to the very thick, cuticularised walls the lumen of these cells is much reduced, forming a narrow tapering cavity at the distal end of each hair. The outer margins of the stomatal furrows are formed by particularly large epidermal cells which overarch the cavities.



FIGS. 9—13.—The stem anatomy of *Bobartia indica.* Fig. 9. Diagram of the distribution of the tissues as seen in transverse section: a, epidermis; b, stomatal furrow; c, chlorenchyma; d, sclerenchyma; e, vascular bundle; f, ground tissue. Fig. 10. Detailed drawing of part of the outer tissues of the stem: a, cuticle; b, sclerenchyma; c, chlorenchyma; d, guard cell; e, scleride; f, parenchyma; g, sclerenchyma. Fig. 11. Surface view of stoma and epidermal cells. Fig. 12. Transverse and longitudinal views of oxalate crystals in the chlorenchyma. Fig. 13. Sclerides from the ground tissue: a, transverse; b, longitudinal.

The stomata are situated at the bottom and sides of the furrows and are somewhat sunken below the level of the adjacent epidermal cells. The stomata are rather small and their mouths are orientated parallel to the long axes of the furrows and of the stem. The guard cells are thin walled and contain chloroplasts. Most of the stomata are anomocytic, but a few appear to have solitary accessory cells inclined at right angles to the pore (Fig. 11).

The tissue beneath and around the stomatal furrows consists of chlorenchyma. The cells are slightly elongated radially but do not form a definite palisade. They are thin-walled and have numerous circular perforations with raised borders. These chlorenchyma cells give a positive reaction for tannin. Irregularly distributed through the chlorenchyma are cells containing crystals of calcium oxalate. The crystals are square or pentagonal when seen in transverse sections but in longitudinal view appear as flat-ended prisms arranged in columns, running for considerable distances through the stem (Fig. 12).

Between the stomatal furrows are supporting ribs of sclerenchyma. This tissue is made up of fibres of varying diameter, with very thick lamellated walls traversed by fine pit canals. The lumen of the outer cells is very narrow, but that of the deeper ones is not so reduced. The sclerenchyma ribs at the base of the stem are wider than those in the upper parts. A small vascular bundle is situated at the inner edge of each of these ribs.

Internal to the chlorenchyma and sclerenchyma is an irregular zone of parenchyma and sclerotic cells, varying in width from two to five cells. The extent of lignification of this zone increases with age and is greatest where the stem leaves the protection of the basal tuft of leaves. Scattered amongst the parenchyma cells are brachysclerides, which although giving a weak lignin reaction, have thick lamellated walls. These sclerides are seen to be lobed in transverse section and the lumen follows internally the contour of the lobes. The walls are perforated by wide pit canals. The sclerides appear to develop by progressive lignification and thickening of chlorenchyma cells.

Bounding the inner vascularised core of the stem is a zone of sclerenchyma some ten cells deep. This is made up of fibres of the normal type, with simple pits with elliptical mouths. In the region of the stem just above the leaves, the thickest and toughest part, there may be an almost continuous system of lignified cells extending from the inner zone of sclerenchyma out to the sclerotic ribs underlying the epidermis.

The centre of the stem is occupied by vascular bundles embedded in a matrix of lignified parenchyma. The vascular bundles are arranged in two series. One lies against the inner boundary of the sclerenchymatous sheath, consisting of both large and small diameter bundles. These bundles have conspicuous caps of sclerenchyma on their inner and outer edges and are somewhat elliptical when seen in transverse section. The second series of bundles is innermost. These are of intermediate diameter and are more or less circular in transverse section. They have a thick sclerenchyma sheath on all sides. The phloem is of the usual monocotyledonous type but the xylem does not show the typical arrangement. The metaxylem consists of vessels of various diameters, all fairly wide, but there are no tracheids present. In transverse section the smaller metaxylem vessels cannot be distinguished from the protoxylem. There are no protoxylem canals.

Parenchyma forms the ground tissue of the centre of the stem. These cells are at first filled with starch, but this is absent in the mature stem. The cell walls eventually become lignified and pitted. Some cells, scattered through the parenchyma, develop extremely thick walls, with almost complete elimination of the lumen, to form brachysclerides. These show numerous simple pits with long, narrow, often branched canals (Fig. 13).

CADABA JUNCEA (Sparm.) Harv.

Cadaba juncea is a broom-like plant which inhabits the more karroid regions of South Africa. The mature plant reaches two metres in height and is stiffly erect, with numerous pungent-tipped branches. There are two distinct types of shoots, the uppermost being pale glaucous-green, circular in section and tapering towards the apices. These become somewhat corky at their lower extremities. The branches at the base of the plant, either arising vertically or extending horizontally, are flattened and covered by a corky bark. In some cases these horizontal branches may form a stiff ribbon some eight centimetres across whilst being only one or two centimetres thick. There is a very abrupt boundary between these two branching systems.

The general structure of a young stem is illustrated by Fig. 14, whilst Fig. 15 shows the detailed structure of the cortex of a more mature stem. The upper green stems of the plant are covered by a very thick cuticle which gives a strong fat reaction. The epidermis is composed of radially elongated cells, the outer and radial walls of which are thick and heavily cuticularised. Thickening appears to take place centrifugally so that the cells develop lamellated caps in which the lumen becomes reduced to a narrow tube. However, the inner tangential wall remains thin and the

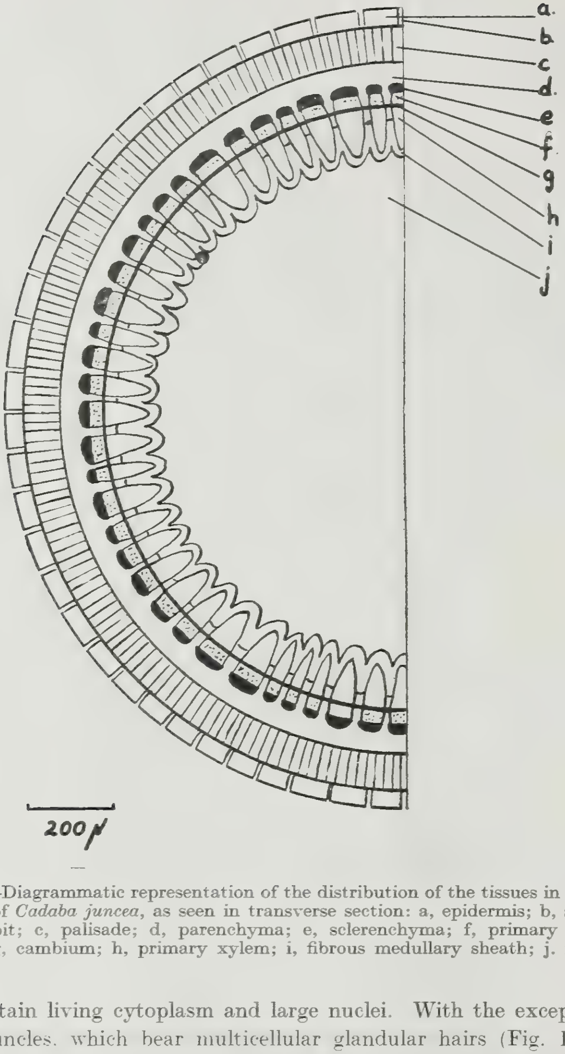


FIG. 14.—Diagrammatic representation of the distribution of the tissues in the stem of *Cadaba juncea*, as seen in transverse section: a, epidermis; b, stomatal pit; c, palisade; d, parenchyma; e, sclerenchyma; f, primary phloem; g, cambium; h, primary xylem; i, fibrous medullary sheath; j. medulla.

cells contain living cytoplasm and large nuclei. With the exception of the peduncles. which bear multicellular glandular hairs (Fig. 16), the epidermis is devoid of emergances.

The stomata are sunken in cylindrical pits, the guard cells lying at the level of the inner limit of the epidermis. The stomatal pits are frequently inhabited by colonies of a unicellular green alga closely resembling *Chlorella*. The mouths of the stomata are orientated at right angles to the long axis of the stem. There are no accessory cells.

The cortex is differentiated into an outer palisade and an inner narrow zone of parenchyma. The palisade is about five cells deep. The cells are elongated radially, somewhat fusiform in shape and with thin walls. There are abundant chloroplasts and most of the cells contain cuboid crystals of calcium oxalate.

In the young stem there is a well-defined zone, about six cells deep, of starch-filled parenchyma underlying the palisade. At maturity this becomes differentiated into an outer region of lignified cells and an inner one of non-lignified cells containing oxalate crystals. Chloroplasts are present in all the cells in the young stem. No myrosin cells occur, as has been reported for some other genera in the Capparidaceae (Metcalfe and Chalk 1950).

The cortex of *Cadaba juncea* is the site of an unusual and interesting process of lignification. In the early stages, nodes of lignin develop on the facets of the isodiametric cells forming the inner parenchyma zone. From these a network of lignification spreads over the surfaces of the cells (Fig. 17). This is connected to and appears to be the point of commencement of the development of a lignified reticulum which permeates the palisade (Fig. 18). This takes the form of anastomosing lignified strands which pass out through the intercellular spaces, finally reaching the base of the epidermis. The strands are at first thin and weakly lignified. Increase in thickness and lignification of the strands proceeds centrifugally from the inner side of the palisade. The areas underlying the stomatal pits are at first unaffected but these, too, eventually become invested by the dense network of lignified strands (Fig. 15).

The stele is bounded by a series of lignified "pericycle" fibres which initially lie opposite the primary vascular bundles. As the stem matures these small irregular groups of fibres become laterally connected by brachysclerides which replace parenchyma cells.

The primary bundles are of the usual type for young dicotyledonous stems. There is a primary phloem within which is a broad cambial zone. There are numerous small xylem groups, each consisting of a single radial row of vessels embedded in fibres. The primary vascular rays are two to four cells wide, of fairly thick-walled, brick-shaped cells with numerous simple pits. The primary rays are persistent, being added to by cambial activity.

The medulla of the young stem consists of large, isodiametric parenchyma cells. At an early stage lignification sets in, although numerous small circular areas of the cell walls are left unthickened (Fig. 19). The

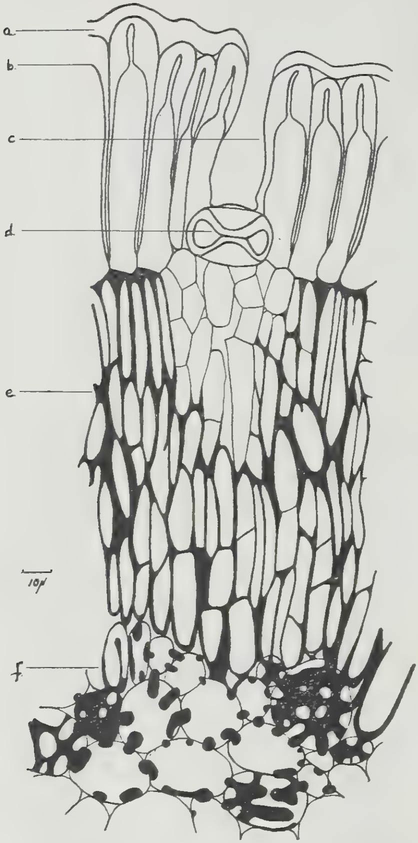


Fig. 15.—Detailed drawing of part of the outer tissues of the stem of *Cadaba juncea*, as seen in transverse section: a, cuticle; b, epidermis; c, stomatal pit; d, guard cell; e, palisade, showing extent of lignified strands; f, parenchyma, showing developing lignification.

cells in the vicinity of the protoxylem groups are the last to become lignified. In the final stages the entire medulla is occupied by cells having very thick walls, perforated only by simple pits (Fig. 20).

The primary stage of development is very short-lived. The structure and development of the secondary vascular cylinder is at first quite normal. Secondary phloem is formed centrifugally, causing distortion of

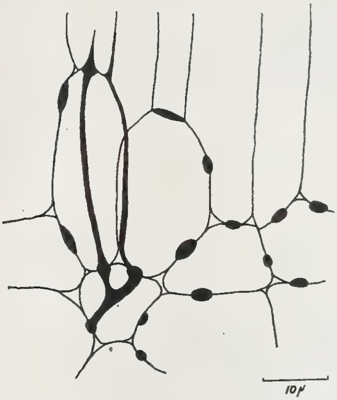
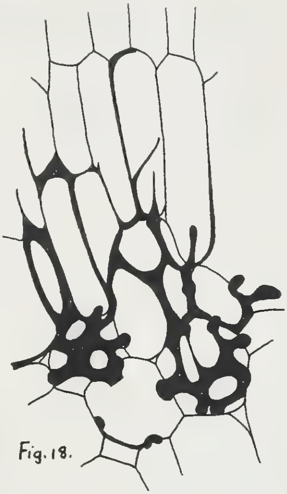


Fig. 17.



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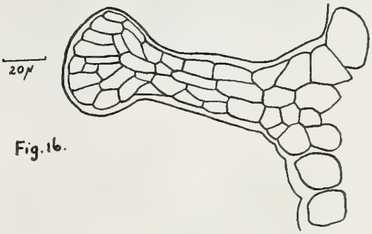

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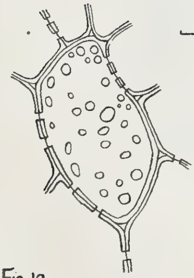

Fig. 19.

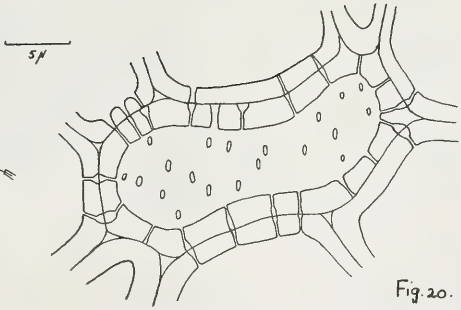

Fig. 20.

Figs. 16—20.—The stem anatomy of *Cadaba juncea*. Fig. 16. Epidermal hair from peduncle. Figs. 17 and 18. Drawings of the inner part of the cortex as seen in transverse section, showing two early stages in the development of the lignified strands. Fig. 19. Parenchyma cell from medulla of young stem. Fig. 20. Highly thickened cell from medulla of mature stem.

the primary phloem. There are no secondary phloem fibres. The differentiation of the secondary xylem from the products of cambial activity proceeds rather slowly. The wood consists largely of fibres, interspersed with a small number of radial rows of vessels. The vessels are pitted, having very numerous small bordered pits with elliptical mouths (Fig. 21). This observation seems to be at variance with the statement by Metcalfe and Chalk (1950) that only simple pits occur. Though there is no raised annular border around the pit mouth, there is a large pit cavity and a conspicuous torus. In some specimens examined there were irregularly scattered tangential plates of parenchyma immersed in the wood.

When the stem reaches a diameter of about three millimetres the first phase of secondary growth ceases and anomalous development commences (cf. Adamson 1936, Metcalfe and Chalk 1950). Cambial activity is initiated in the region of the pericycle, in small patches which extend partially around the original woody cylinder (Fig. 22). Phloem is formed centrifugally and xylem centripetally. This causes considerable distortion of the underlying secondary phloem although in the early stages it hardly disturbs the outer tissues. As development proceeds, new wood is continually added to one side of the stem, the initially separate patches of cambium merging into an arc. Growth of a periderm accompanies expansion of the stele so that an unbroken secondary cortex is maintained. The new wood is rather more porous than the first-formed secondary xylem and the broad vascular rays often have a wavy appearance in transverse section.

Development of this pericyclic growth eventually ceases and cambial activity is renewed beyond the phloem. The new cambium now occupies a more restricted arc and the stem assumes a distinctly eccentric appearance. This process is repeated many times, new material being continually added to one side of the stem so that a broad woody ribbon is formed (Fig. 23).

Periderm formation commences just prior to the onset of pericyclic cambial activity and is seen as longitudinal corky fissures in the surface of the green stem. These become more numerous and extensive, anastomosing, and eventually, on the old main stem, covering the entire surface. The periderm is of epidermal origin (Fig. 24). Divisions commence in the inner half of certain epidermal cells, causing the accumulation of phellem within the lumen of these cells. As divisions proceed, the inner tangential walls of the epidermis are broken and displaced by phelloderm. Eventually the whole epidermis is lifted, the empty cuticularised walls curling outwards above the periderm. Periderm formation initially takes place in narrow sectors of the epidermis only, there being a very sharp boundary

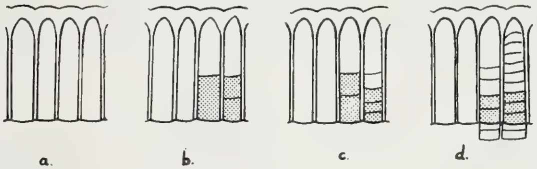

Fig. 24.

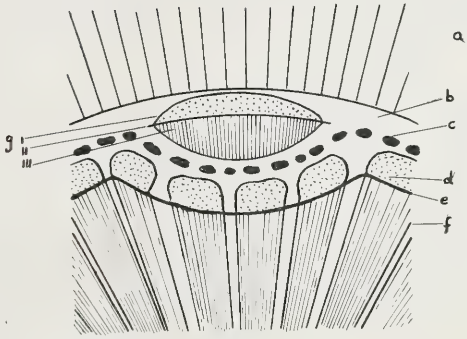

Fig. 22.

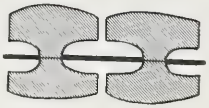

Fig. 21.

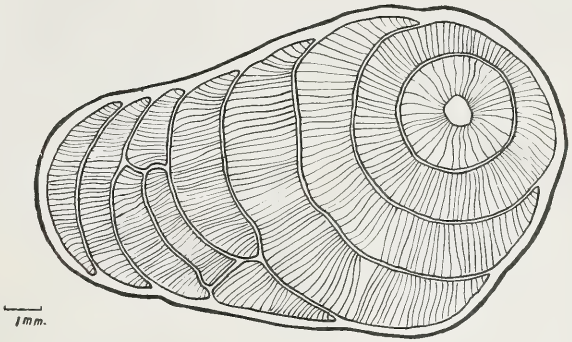

Fig. 23

Figs. 21—24.—The stem anatomy of *Cadaba juncea*. Fig. 21. Diagrammatic longitudinal section through bordered pit of xylem vessel. Fig. 22. Diagrammatic representation of the initial stage of anomalous secondary thickening: a, palisade; b, pericyclic parenchyma; c, pericyclic fibres; d, secondary phloem; e, cambium; f, secondary xylem; g, anomalous secondary bundle: i, phloem; ii, cambium; iii, xylem. Fig. 23. Drawing of transverse section through mature stem. Fig. 24. Diagram to show the mode of periderm formation: a, normal epidermis; b and c, commencement of meristematic activity; d, establishment of phellem, phellogen and phelloderm.

between phellogen and undividing cells. The mature stem has a broad secondary cortex, due to phelloderm lying directly over the secondary phloem, although the phellem does not accumulate to any very great extent.

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